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Patterns in the Distributions of Grassland Birds, Landscape Elements and Prey: A Case Study in Eastern Wyoming

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Abstract

PATTERNS IN THE DISTRIBUTIONS OF GRASSLAND BIRDS, LANDSCAPE ELEMENTS, AND PREY: A CASE STUDY IN EASTERN WYOMING

by Tammy L. Hamer

Chairperson of the Supervisory Committee:
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ABSTRACT: The landscape of the Great Basin region has changed dramatically in the last 150 years, particularly in areas where water is available for irrigation farming. This has resulted in a fragmented landscape with fewer large tracts of grassland and shrubsteppe. The severity of land use conversion to agricultural land is patchy in eastern Wyoming, resulting in varying degrees of fragmentation and disturbance. This variation in the severity of anthropogenic changes to the landscape offered an ideal platform for a regional spatial analysis of grassland birds. This study was conducted between 1994 and 1998 at 29 bird survey locations. Precluding an analysis of spatial patterns in grassland birds, the hypothesis that grassland bird distributions in eastern Wyoming

were independent of physical and biological processes was tested using a null spatial model. A null spatial model randomizes ecological data to produce a random spatial pattern in the absence of mechanisms. Mean species richness estimates were generated randomly for survey locations under a *Monte Carlo* resampling technique and compared to observed mean bird richness. Species richness deviated from the null model, which was spatially neutral with respect to the distribution of individuals within the landscape, prompting further exploration into underlying patterns of grassland bird species richness on the landscape. I compared species richness of grassland birds to landscape amount and configuration and grasshopper density and richness. These data were used to develop models of species occurrence using site-specific landscape variables and prey. The landscape was quantified using satellite-based imagery. Mean grasshopper density and richness was estimated at each bird survey site and compared to the species richness of grassland birds. My results suggest a relationship between habitat amount and habitat arrangement and the number of grassland birds that co-occur in an area.

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INTRODUCTION

Over the past three decades, grassland birds have experienced steeper declines than any other ecological bird group in North America (Knopf 1994). This adds to a growing concern over loss of species resulting from anthropogenic changes to the landscape (Wilson 1988; Finch 1992). Conversion of prairie to row crops and the intensified management of agricultural fields have greatly reduced the ability of grassland birds to successfully breed. Studies at the population level (Noss 1990) have addressed the decline of grassland birds (Best 1978; Herkert 1993; Johnson and Temple 1990; Knopf 1994; Line 1994; Wray 1982), but few studies have attempted to examine grassland bird dynamics at broad geographic scales (Mauer 1994). Ecologists have acknowledged the need for more broad-scale (i.e. macroecological) research (Brown 1995). But broad-scale surveys of organisms are scarce, and computers capable of processing large data files such as satellite images are relatively recent advances in technology. With the paucity of information at the regional and sub-regional scale, land management and policy decisions are increasingly being made at these levels based on little or no research explicitly conducted at these scales. Furthermore, most grassland bird studies have focused on population dynamics or habitat occupancy patterns for selected species with little attention given to shifts in community structure. If, in fact, the documented declines in local

grassland bird abundance were widespread, then these changes would be expected to manifest as changes in species composition at the community level.

Community ecology continues to question whether species assemblages express patterns that exhibit ecologically based processes, or if assemblages of species are random collections of individuals devoid of ecological processes. This study was designed to investigate the relative importance that landscape heterogeneity and prey resources have in explaining variation in grassland bird richness. The approach was to analyze species richness of grassland birds at a variety of landscapes that varied in the degree of anthropogenic disturbances. However, prior to investigating the role that specific factors may have in explaining grassland bird richness, it seemed prudent to first demonstrate that the observed pattern is not simply a function of random processes.

NULL MODEL

Null spatial models are conceptual or mathematical formulations devoid of ecological process. The null model randomizes ecological data by holding certain elements constant and allowing other elements to vary stochastically, producing a random pattern in the absence of abiotic and biotic mechanisms (Gotelli and Graves 1996). Null models do not in themselves elucidate a particular mechanism, but the null model can facilitate the detection of underlying spatial patterns (Gotelli and Graves 1996).

This research first developed a null spatial model in order to test if the spatial distributions of grassland bird species in eastern Wyoming deviated from random. The null spatial model that I tested was neutral with respect to species response to the landscape, predator-prey and herbivore-plant interactions, and intraspecific and interspecific competition. Rejection of the null hypothesis implies that grassland birds are selecting sites based on some combination of abiotic and biotic variables such as habitat, predator-prey interactions, and intraspecific and interspecific competition (Caswell 1976).

LANDSCAPE

The landscape of the Great Basin region has been severely altered and converted into agricultural land. Once ploughed and converted to agricultural land, it is unlikely that the land will return to its native community. Eastern Wyoming has had a long history of grazing, fire, and invasion of exotic plants that further altered the grassland-shrubsteppe ecosystem of this region. The agricultural productivity in this region, however, was largely limited by rainfall and the availability of water. Hence, in eastern Wyoming, the severity of anthropogenic changes to the landscape varied spatially. The conversion of grassland and shrubsteppe communities to agricultural fields in eastern Wyoming has resulted in various degrees of fragmentation. Changes in the amount and arrangement of habitat on the landscape can influence avian

species distribution and abundance (Ambuel and Temple 1983; Bolger *et al.* 1991, 1997; Vander Haegen 1999).

BIRDS

Grassland birds have undergone substantial population declines (Askins 1993; Knoph 1994; Herkert 1995; Peterjohn and Sauer; 1999). The most likely factors associated with these declines are loss and degradation of native prairie (Herkert *et. al.* 1996). The loss and conversion of formerly extensive tracts of grassland-shrubsteppe habitat has reduced the habitat available to avian species for breeding. Changes associated with loss of habitat and increased fragmentation include a decrease in the total amount of habitat, a decrease in the average size of the patches, increased patch isolation, and increase in edge. These landscape effects can have severe consequences for grassland birds. Over half of grassland bird species have experienced long-term population declines according to the Breeding Bird Survey (Robbins *et al.* 1993; Peterjohn and Sauer 1993). Therefore, grassland birds have become a management concern (Rodenhouse *et al.* 1995).

GRASSHOPPERS

Analysis of the spatial pattern of organisms can provide insights into population dynamics and ecological interactions. Spatial and temporal patterns of most organisms rely, at least in part, on variation in primary prey species (Pimm 1991). For this reason, an analysis of the spatial components of variation in grasshopper abundance and diversity may provide valuable insight into the population fluctuations of grassland birds (Table 1).

Grasshoppers have high nutritional value, exceeding 50% crude protein (Ueckert *et al.* 1972; DeFoliart 1975). Protein is an important component in the diet of birds, especially during the breeding season (Robbins 1981), and studies have shown that grasshoppers are an important prey item for grassland birds (McEwen 1989). For example, 29% of the diet biomass of birds in four grassland/shrubsteppe habitats in North America consisted of orthopterans (Wiens and Rotenberry 1979). Other insects besides grasshoppers have been linked to birds. For example, Pearson and Carroll (1998) found that the number of butterfly species was a useful indicator for bird species in North American and Australia.

A number of studies have examined reproductive success by experimentally manipulating food abundance (Murphy and Haukioja 1986; Martin 1987; Boutin 1990; Simons and Martin 1990); and many researchers have documented the response of birds to natural changes in food availability (Zack and Falls 1975;

Anderson 1977; Sealy 1980; Marr and Raitt 1983; Strehl and White 1986; Miller *et al.* 1994). For example, Anderson (1977) found higher fledgling success in House Sparrows (*Passer domesticus*) in response to cicada outbreaks. Marr and Raitt (1983) found that Cactus Wrens (Campylorhynchus brunneicapillus) increased clutch size in abundant grasshopper years. Miller *et al.* (1994) noted a higher mean clutch size during a year of high grasshopper density for savannah sparrows (*Passerculus sandwichensis*) in Alaska. However, at a macro-scale, bird surveys and insect surveys are rarely conducted at a single survey site, making the analysis of insect influence on bird communities difficult at broader spatial scales.

In Wyoming, there are >100 species of orthopterans. Many species vary in abundance, size and hatch date. An analysis of grasshopper abundance and richness may play a role as bioindicators of grassland bird richness (Table 1).

SUMMARY

Studies conducted at broad spatial scales are appropriate for questions regarding the cumulative effects of land management activities on target species at the regional or sub-regional level. However, there are difficulties in conducting controlled replicated experiments at this scale, such that most inference will be based on corroborating evidence (i.e. correlations) rather than true experimentation. Notwithstanding, the need to take a top-down approach,

especially when various broad scale databases are readily available for macroecological research, has the potential to be very valuable and may provide insights into regional land management decisions that may support diverse avian communities.

Until recently, most research on grassland birds was largely non-spatial. For example, the relationship between organisms and resources, and the spatial pattern between organisms and their resources had been largely ignored. Moreover, ecological studies at a regional or subregional scale are scarce, where broad patterns may exist but are not explicitly addressed. With the availability of extensive databases for birds, grasshoppers, and satellite imagery, research at a macroscale is possible where historically it was not. My study addresses three major questions. First, does the spatial distribution of grassland bird species in eastern Wyoming deviate from a random distribution? Second, can landscape composition and configuration derived from satellite imagery explain patterns in grassland bird species richness in eastern Wyoming? Third, does the density or richness of grasshoppers constrain grassland bird species co-occurrence? The investigation of these questions led to the development of models for species co-occurrence in grassland-shrubsteppe ecosystems of the Great Basin region. I discuss the observed species richness patterns in terms of the relationship to the spatial distribution of prey resources and habitat patches.

STUDY AREA

The study area was eastern Wyoming, covering approximately 200,000 km^2 (Figure 1, 2). I selected Wyoming because little research has been conducted on grassland birds in the west, because BBS routes were well distributed throughout the state, and because of the extensive grasshopper database that exists for Wyoming. Eastern Wyoming had little topographic relief. The primary vegetation in this region consisted of shortgrass and mixed grass prairie, sagebrush, and scattered inclusions of forest vegetation associated with riparian and higher elevation sites. The primary land uses in this region were open rangeland and agricultural cropland. The two predominant grass types in shortgrass and mixed grass prairies are Blue Gramma (*Bouteloua gracilis*) and Buffalo Grass (*Buchloe dactyloides)* (Knopf 1988).

METHODS

T he approach taken in this study was: (1) define landscape units as study sites, (2) create a random distribution of species to these sites based on empirical data to test if patterns in avian species richness are driven by ecological mechanisms, (3) assess potential correlations between avian species richness

The overall level of agreement between the map and ground-truthed points was 79.6% (Analysis, Wyoming Gap, 1996)

The BBS route coverage was overlayed on the GAP thematic vegetation coverage, using the software package *ArcView 3.2 (Environmental Systems Research Institute (ESRI))*. The Gap thematic map was then clipped with the BBS route coverage, creating a thematic vegetation-class buffer of one km around each BBS route. A buffer of this size was selected because this would sufficiently include the entire breeding territory size of most grassland birds, even in marginal habitat (exceptions are Prairie Falcon (*Falco mexicanus*), Swainson's Hawk (*Buteo swainsoni*), Northern Harrier (*Circus cyaneus*), Ferruginous Hawk (*Buteo regalis*) and Short-eared Owl (*Asio Flammeus*)). Inspecting the vegetation types that surrounded each route within the 1-km buffer identified routes containing >3% grassland habitat.

The next criterion for route selection was completion of survey years. I selected the time period of 1994-1998 to coincide with other datasets. Routes were selected if they were surveyed in 2 or 3 years within the 5-year window. For each route, I averaged the number of birds observed across years, by route, using 2 or 3 years within each time period. For routes with greater than 3 surveys completed in a time period, I selected years to include for analysis by centering on the midpoint of the time period, 1996. Centering on a midpoint was an attempt

to minimize the variance among years. Years to be included in analysis were selected for each route in this order: {1996, 1997, 1995, 1998, 1994}, until 3 completed surveys were reached. The culmination of these two criteria resulted in 29 BBS routes for analysis (Figure 2).

GRASSLAND BIRD SPECIES POOL

The grassland species pool composition was defined by combining lists of grassland bird assemblages from the published literature (Johnsgard 1970; Samson and Knopf 1996; Peterjohn and Sauer 1993). To establish a species' assemblage, as those found in the literature, breeding habitat nest type, migration form, and nest location were considered (Peterjohn and Sauer 1993). This grassland species pool was refined to include only those species that had a potential for being observed in the study area. This refinement was achieved by including those species from the literature-derived species pool that were actually observed along any BBS survey route in eastern Wyoming at any time during the 1966-1998 period. Therefore, the grassland species pool included all species that had a likelihood of being detected in eastern Wyoming (Table 1).

GENERATING A NULL MODEL

The simplest explanation for species richness is that individuals occur randomly in space. (Diggle 1983; Solow and Smith 1991) If individuals occur randomly across the landscapes, then there is no need to search for explanations of

species richness patterns across the landscapes (MacNally 1990b). This was tested with a null model.

To generate a biologically neutral distribution of species to landscapes, species occurrence data from the BBS were downloaded from the PWRC web site and incorporated into a *species by route* matrix (Simberloff and Connor 1979). Each row of the matrix represented a different species and each column represented a different BBS route (Appendix A). Each cell in the matrix (a_{ij}) denotes the average number of birds of each species i observed on route j over a 2 to 3 year period. A separate matrix was generated for each of the two time periods. In addition, row and column totals were calculated such that R_i equals the sum of the average abundance of species i across j routes and C_j equals the sum of average abundance on route j across all species.

The function of the null model was to construct an empirical distribution (ED) of route richness under the null model assumptions for comparison to the observed richness on a per route basis. To achieve this, a program read two files containing the row (R_i) and column (C_j) totals of the *species by route* matrix in a two-dimensional array, and randomly created a hypothetical two-dimensional array whose row and column sums equal to the observed values. Constraining the random assignments by fixing row and column totals was necessary since the hypothesis that all species have an equal likelihood of occurring on all

routes is almost certainly false. By incorporating a distribution structure into the model, the simulations were more realistic, which created a more conservative test for spatial randomness (Gotelli and Graves 1996). With no structure in the null model, the null model would be easily rejected but the strength of the test would be questionable (Gotelli and Graves 1996). Cell values were allowed to vary stochastically, subject to the restriction that placing a new value into a cell cannot cause the column total or the row total to exceed the observed values. R_i and C_j values were rounded prior to input into the null model program for the purpose of generating integers values.

SIMULATIONS

The serial algorithm used to generate the null model:

(1) The total number of individual birds observed in any one-time period defined the pool from which random assignments were made.
(2) Randomly select a cell in the species by route matrix.
(3) Can individual x be assigned to that cell while maintaining R_i and C_j from the empirical distribution in the *species by route* matrices?
    a. Yes - individual is assigned to that cell and a new cell is selected.
    b. No – retain original value and select another cell.
(4) Continue until row and column totals are maintained.

Under a *Monte Carlo* resampling plan (Manly 1998), I generated 10000 simulated *species by route* matices under the null model assumptions. Expected species richness for each BBS route *(j=1-29)* was estimated by converting each simulated *species by route* matrix into a binomial presence-absence matrix and

summing the presences within each route. I computed species richness $\hat{S}_{kj}$ where k indexes a specific realization from the 10000 simulations and *j* indexes BBS route. The mean ($\overline{S}_{.j}$) and standard devation of 100 simulations for each route *j* was calculated.

TESTING FOR DEVIATION FROM A NULL MODEL

The spatial nature of these data violates assumptions of classical statistics, potentially producing misleading results. I therefore used a nonparametric *Monte Carlo* test. The probability of deviation from the null model was calculated using a *Monte Carlo* test that followed a procedure defined by Diggle (1983):

> Let $\hat{S}_{1j}$ be the observed species richness on route j. Define d_k to be a measure of squared deviation between the observed richness (k = 1) or the simulated richness (k = 2....101) and the mean simulated richness. With the overall mean of 100 simulations, $\overline{S}_{.(j)}$ and $\hat{S}_{k(j)}$ as the species richness in the k^{th} simulation and the j^{th} route, then
>
> $$d_k = \int [\ \overline{S}_{.(j)} - \ \hat{S}_{k(j)}\ ]^2 \, dn$$
>
> Let m be the total number of simulations plus the observed data (m = n + 1), then define r_k as the rank of d_k such that the probability of observing the rank $r_1 > R$ given by r_1/m.

Given the above test, if the observed species richness fell outside the simulated distribution curve at a $p < 0.5$, then the observed richness exceeded that which could be expected by chance and the null model was rejected.

LANDCOVER CLASSIFICATION

Conditional on rejection of the null model, species richness patterns were evaluated for potential correlation with landscape heterogeneity. I used Landsat 5 Thematic Mapper (TM) data from 7 scenes to develop land cover classes for the study area. Landsat scenes were acquired for late Aug-October 1996, during senecence of shrubs and deciduous trees, but prior to snowfall. Computer processing of the remotely sensed imagery to classify the landscapes into habitat cover types based on the spectral reflectivity data from seven sensors was achieved using *ERDAS Imagine* 8.4 image processing software on a SUN SPARC 10 workstation. Classification is the process of sorting pixels into a finite number of individual classes based on their data file values. Landsat 5 TM satellites have 7 sensors; each sensor is sensitive to a specific portion of the wavelength curve. Measurements by these sensors are collected at a 30 x 30 meter resolution. Therefore, the output image is a raster data file containing 30 x 30 meter pixels; each pixel contains 7 layers of data and each layer represents the spectral reflectivity from a specific portion of the wavelength curve. I used all seven bands for classification. These bands include the blue (0.45 - 0.52 μm), green (0.52 - 0.60 μm), red (0.63 - 0.7 μm), near infrared (0.76 - 0.90 μm), mid-infrared

(1.55 - 1.75 μm), thermal infrared (10.40 - 12.50μm) and a second mid-infrared band (2.08 - 2.35μm).

I used a hybrid classification approach by combining techniques of unsupervised and supervised classification. Unsupervised classification is the process where the computer uses the spectral distances to iteratively separate each pixel and assign it to classes of similar characteristics. One hundred cluster classes were specified, at a 0.985 convergence. For each cluster, a signature is created. I assigned each cluster to a vegetation cover class (Table 3). I used high-resolution color-infrared aerial photography (NAPP 1:24000 scale) as reference data, combined with field data, to classify the clusters into covertypes. Once each cluster was assigned to a land cover class, I ran a supervised classification. I chose the maximum likelihood (ML) classifier as the decision rule. The ML classifier bases classification on the probability that a pixel belongs to a particular class. This parametric classifier was considered to be the most accurate of the classifiers when the data are normally distributed. A modified Anderson level II classification system was used (Table 3). These thematic land cover images were converted to GRID and incorporated into *ARC/INFO* (Environmental Systems Research Institute, Inc.).

The accuracy assessment allows one to compare certain pixels in the thematic raster layer to reference pixels, for which the class is known. This is an organized way of comparing the classification with what is believed to be

"truth". I used a stratified random sample of 500 pixels. These classified pixels were evaluated for accuracy by comparing the classified pixel against the cover type that was actually present in that test pixel. The actual cover type was determined using large-scale aerial photos, and, occasionally with assistance from the existing cover type map of Wyoming GAP. The aerial photography for the accuracy assessment was not used to train the classification, to maintain independence.

LANDSCAPE METRICS

Measurements reflective of the spatial heterogeneity of habitat types at the landscape level (i.e. metrics across all land cover types) and at the class level (i.e. metrics specific to only one cover type) were calculated using FRAGSTATS, version 3.01 (McGarigal and Marks, 1995). Fragstats explicitly measures characteristics of landscape structure.

Landscapes were extracted at a specified 1.0 km (radius) from the BBS route, thereby all measurements were calculated at this buffer distance from each route. Each landscape was quantified to landscape pattern metrics including amount of each habitat cover type, habitat diversity and richness, amount of edge, average size of patches, contrast (subjectively defined measurement of contrast between two cover types), interspersion-juxtaposition (the extent to

which cover types are clumped), and fractal measurements (reflection of patch shape) (see Table 4).

AVIAN DATA

The U.S. Fish and Wildlife Service's Breeding Bird Survey (BBS) program supplied the data used to select study sites and to characterize the grassland avifaunal distributions in eastern Wyoming. BBS provides a spatially and temporally extensive representation of avian species richness and abundance (Mauer 1994). It is the most long-term database of richness and abundance in birds of North America that exists, beginning in 1966 and continuing today. Currently, there are over 4000 designated BBS routes. During June of each year, a competent observer drives a 39.4-km route, stopping every 0.8-km (a total of 50 stops/route). At each stop point, the observer records all birds seen and heard within a 0.4-km radius for 3 minutes; see Droege (1990) for details.

A 5-year window of BBS data, centered on 1996 to be compatible with the year of the satellite imagery, was used to calculate a mean species richness. A time-window of 5 years was selected to increase the detection of rare species and to average the variance in yearly surveys. Only routes that were deemed acceptable by BBS administrators were used. Acceptability is based on competence of the observer, weather conditions at time of survey, and survey date must be within the peak of the breeding season for birds.

ESTIMATING SPECIES RICHNESS

The major methodological problem encountered when species richness is compared at different locations is the variation in detection probability among species. In population studies, the need to use probability models to estimate the proportion of animals not detected at sampling occasion is widely used. However, community-level studies continue to use unadjusted raw counts of species, and do not take into account the fact that not all species are likely to be detected with the same probability. The application of capture-recapture estimators to estimating species richness is a fairly straightforward extension of population estimates, thus generating more realistic estimates of the number of species (Boulinier *et al.* 1998; Nichols *et al.* 1998; Hines *et al.* 1999).

To characterize grassland avifaunal assemblages in eastern Wyoming, observed values for the number of species and the number of individuals were obtained from the BBS database archives. To estimate relative species richness along these 29 routes, I used the software program COMDYN (Hines *et al.* 1999; Nichols *et al. 1998*). This program was written based on the methods described by Burnham and Overton (1979) and described in application to BBS data in Boulinier *et al.* (1998). COMDYN used a closed population model to derive estimates. The sample community is considered "closed" to local extinction

and colonization for a relatively short period of time over which species presence-absence data are collected. Individual species in the community context corresponds to individual animals in a population context, therefore the detections of species in a sample corresponds to captures of individual animals.

In this approach, I substituted species for individuals, and each species is identifiable as if they were marked, which is why a capture-recapture application can be extended to estimating species richness. Five quadrates along each BBS route were used as the capture occasions. Calculated outputs from COMDYN were estimates of species richness ($\hat{S}$) for each route and a standard error ($\pm$ SE) on the estimates based on 200 bootstrap iterations.

In summary, the program used a robust capture-recapture approach on presence-absence data for each species to estimate the number of species not detected. The best estimates for BBS data are based on model M_h, which specifically addresses the heterogeneity in detection probability among species for estimates of richness using a jackknife estimator (Boulinier *et al.* 1998).

GRASSHOPPER DATA

Grasshopper (Orthoptera: Acrididae) surveys have been conducted since the late 1940's across much of the western United States. Surveys are organized by the USDA Animal and Plant Health Inspection Service (APHIS) and conducted

by trained observers along roadsides. Surveys are conducted over a 3-4 week period starting around 15 July, therefore counting grasshoppers in the late nymphal and early adult stages. Surveys estimate abundance of grasshoppers by counting all grasshoppers in a visual 1 square meter grid. Since 1988, in addition to grasshopper abundance estimates, a sweep-net survey has been used for identification of grasshopper richness. Therefore, both density and diversity of grasshoppers can be used for analysis as potential bioindicators of grassland bird richness.

Grasshopper data were downloaded from the University of Wyoming. These data were the results from the USDA- Aphis grasshopper survey and included total grasshopper per square yard as a density measure, and the grasshopper species collected at each survey sites across eastern Wyoming from 1994-1997. The 1998 grasshopper survey was incomplete and therefore unsuitable for analysis. I selected this time frame to coincide with my grassland bird data set and other data in subsequent analysis. This original dataset had more than one record for every survey site; the number of records for a site corresponded to the number of species collected at that survey location. From this dataset, I derived a new dataset that characterized each survey point by its geo-reference coordinates, density of grasshoppers, and the total number of species collected at that point. This query was necessary in order to have each geo-referenced survey location as only one record in the database. These data were brought into a GIS to create a

point coverage. This point coverage was used as the base map to spatially interpolate the grasshopper density and diversity for a 30 x 30 meter grid across the eastern half of Wyoming. Inverted distance weighting (IDW) was used for the interpolation. IDW uses the nearest survey points to interpolate an estimate of grasshopper density and diversity, weighted by the Euclidean distance to that point such that closer points are weighted more heavily then farther points. Interpolation was necessary because there was not a direct relationship between grasshopper survey points and bird survey sites.

DIGITAL COVERAGES/METADATA

- The original BBS route coverage was an *ESRI ArcInfo* vector coverage (metadata A).
- The BBS route coverage had to be re-projected into the corresponding Universal Transverse Mercator (UTM) coordinate system (metadata B)
- Grasshopper survey locations and survey data from a dbase (.dbf) spreadsheet file (metadata C) were used to create four spatial *ESRI ArcInfo* point coverages (metadata D).
- Grasshopper point coverages were used to create ArcInfo Grid coverages of grasshopper density/year across eastern Wyoming (metadata E).
- Grasshopper grid coverages were used to create an average grid of grasshopper density across years (metadata F).
- Grasshopper point coverages were used to create ArcInfo Grid coverages of grasshopper diversity/year across eastern Wyoming (metadata G).
- Grasshopper grid coverages were used to create an average grid of grasshopper diversity across years (metadata H).
- Landsat 5 TM satellite images: Path 33, Row 31; Path 34, Rows 29-31; and Path 35 Rows 29-31. All images we georeferenced and rectified to UTM, Zone 13, Nad83. (metadata I)

PCA/ REGRESSION/PARTIAL REGRESSION ANALYSIS

Landscape metrics

To alleviate problems of multicollinearity among explanatory variables, I ran a Principle Components Analysis (PCA) using SAS statistic package (PRINCOMP procedure) on all generated landscape metrics. If a small number of principle components explain a large amount of the variability in the metrics, such principle components can be a reasonable representation of the data. The problem is, often these principle components lack biological interpretation. I ran a multiple linear regression with estimated species richness as the response variable and the first two PCA's as explanatory variables.

Class-level metrics

Multiple linear regression was used to analyze the relationships between species richness grassland habitat amount and arrangement. In the absence of an *a priori* set of models, all possible combinations of predictor variables were included. I used Akaike Information Criteria (AIC) to select the best models based on the average weight of each model.

RESULTS

NULL MODEL

Approximately 40 BBS routes in eastern Wyoming traverse grassland bird habitat. Of these 40 routes, twenty-nine BBS routes met the habitat and survey year criteria. Twenty-six of the 29 routes were surveyed 3 or more years in both time periods. These 29 routes were used in the subsequent analysis (Figure 2). The definition of a grassland species source pool resulted in a grassland bird species assemblage that contained 28 species (Table 1).

The observed species richness across the 29 routes was highly variable (Table 5). A minimum species richness of 4 and a maximum species richness of 17 were observed during the 1994-1998 time period. The mean annual number of individuals observed across all 29 routes was 10,783.

The *Monte Carlo* test indicated that grassland bird distribution across the 29 routes significantly differed from a random distribution. Nineteen out of 29 routes deviated from the null in time period 1994-1998 ($p < 0.05$) (Table 5). All routes that significantly deviated from the null were routes in which the observed species richness was lower than expected based on the simulations. Only 1.5 routes would be expected to deviate from the null if the distribution of grassland bird was purely random at the $p < .05$ level.

SPECIES RICHNESS ESTIMATES

Estimates of species richness from COMDYN (Hines *et al.* 1998) varied from a minimum of 4 to a maximum estimate of 17 along each of the 29 BBS routes (Figure 3). There was not a lot of variation on the estimates. The mean estimated species richness was 8.569 ± SD 3.012.

LANDCOVER CLASSIFICATION

Based on 501 stratified random pixels (table 6), overall classification accuracy was 81% at an Anderson level I, and about 78% at an Anderson Level II (Anderson *et al.* 1976) (Table 7). The kappa statistic was 0.72 at Anderson level II (Table 7). The accuracy did vary by cover types. The best performance was in the urban, water, forest and row crops. The most confusion was between grassland and shrubland, indicative of the gradient between these two classes in the study area.

BIRD AND LANDSCAPE ANALYSIS

Landscape

I retained the first two PCA axes, which explained 66% and 15% of variation in landscape metrics, respectively. These first two PCA's cumulatively captured 81% of the information contained in the landscape metrics. The factor loadings on these two principle components were well distributed among most of the

metrics, making biological interpretation difficult. Regardless, there was interest in the explanatory power of the landscape metrics. The first two PCA axes were used as predictors in a multiple linear regression analysis. The PCA axes were poor predictors of species richness ($R^2 = 0.04$, $p = 0.579$, $df = 28$, see Table 9).

Grassland Habitat

Based on the results of the linear regression analysis, total amount of grassland habitat and the estimated number of grassland bird species were correlated (MSE=7.95, $R^2 = 0.16$, $p = 0.0343$, see Figure 6).

Model selection procedure:

All possible combinations of 11 grassland habitat amount and structure metrics were used in a model selection procedure. This resulted in 2048 different models. The models with an AICc <2 are considered highly competing models. This procedure resulted in 9 highly competing models (Table 10). With the high degree of model selection uncertainty on the set of models that I ran, no single model should be used to base inference. Therefore, to minimize the risk of spurious results, inferences were based on the entire set of models run. This is a more robust method of inference when a high degree of model selection uncertainty exists. All regressor variables were weighted by each AICc model weight for which that variable appeared. Once all regressor variables were

weighted according to there relative contribution across all models run, the variables were rescaled between zero and 1. The results indicate the contrast weighted edge density (CWED) had the most explanatory power of the variables (Table 11). Interspersion Juxtaposition (IJI) had the second best explanatory power, followed by grassland area (GA).

Bird and Grasshopper Analysis

An average estimate of grasshopper density across years 1994-1997 was estimated using IDW across eastern Wyoming (Figure 4). An average estimate of grasshopper richness was calculated using IDW across eastern wyoming (Figure 5). These two spatial grids were used to calculate the mean grasshopper density and grasshopper richness as explanatory variables of grassland bird species richness. Multiple linear regression results indicate that grasshopper density ($R^2 = 0.0059$, $p=0.6926$)and richness ($R^2= 0.0095$, $p=0.6152$) did not explain much of the variability in grassland bird species richness (Table 8).

DISCUSSION

To gain a more comprehensive assessment of avian response to human disturbance of the landscape, biogeographical studies are needed. Unfortunately, it is often impractical for individuals to collect the necessary data to perform such broad scale investigations. For this reason, it is necessary to rely on the coordination of independent efforts to search for broad-scale patterns and trends. The BBS data, with noted limitations, does provide the most broad-scale survey of any non-human species. The analysis approach used here, namely focusing on presense/absense data and *estimating* species richness, was an attempt to minimize many of the problems associated with the use of BBS data, most notably the problems associated with detection probability.

The null spatial model test results indicated that the spatial distribution of grassland avifaunal species across eastern Wyoming is not random. These results suggest less flexibility in where birds locate during the 1994 -1998 time period. The rejection of the null spatial model justified further investigation into specific mechanisms that may underlie non-random patterns.

Describing species distribution patterns and uncovering the mechanisms underlying these patterns is critical because intensified land use continues to alter the availability, quality and distribution of habitat. Even with the paucity of information at the regional and sub-regional scale, land management and policy

decisions are being made at these levels, forcing land managers to extrapolate beyond the scope of the available data. To address the cumulative effects of human-induced disturbances, a regional or macroscale approach to wildlife research can offer a relatively fast and inexpensive way to address current conservation issues (Brown 1995). To date, much of the focus in wildlife research has been on single species at the local scale. The research discussed here has taken a community level approach and examined both richness and distributional patterns at the landscape scale.

The findings of this study that landscape metrics explained very little of the variability in species richness was not too surprising. These metrics are measurements across all landscape classes. In addition, species richness quantifies simply the number of species in a given area. Species will respond in unique ways to the landscape. Considering the fact that the response variable is species richness, perhaps it is not surprising that as a collection of species, there is not a pattern in the response to metrics reflecting the structure of various land cover classes. The findings of this study were that landscape metrics, at this scale, have little influence on the number of grassland species. Due to the exploratory nature of this study, this finding by no means suggests that the landscape composition and structure do not influence grassland birds. The findings here prompted further exploration into the influence of grassland habitat as predictor variables of grassland bird species.

Total grassland area was a significant predictor of the number of grassland bird species. This result suggests that conserving grassland area would be beneficial to an assemblage of grassland birds. If conservation goals are to increase the numbers of grassland bird species, than conservation of native grassland habitat could achieve that goal.

The various metrics representing the composition and structure of grassland habitat resulted in a high degree of model selection uncertainty. However, up to 50% of the variability in grassland bird species richness was explained by the habitat metric models. Contrast weighted edge density had the greatest amount of explanatory power. Contrast edges could provide habitat to a suite of species that may not be found in more homogeneous landscapes. Therefore, it is not too surprising that the amount of contrast between the grassland habitat and the adjacent land cover class could influence the number of species in an area. This finding is supported by that of Penhollow and Stauffer (2000), where they found that edge species and habitat generalists are selecting landscapes with higher contrasting edges. The contrast edge, thereby, offers habitat that a diversity of species can exploit, but perhaps at the expense of interior species and specialists. Surrounding landscape features are important predictors of bird occurrence (Saab 1999), and other research has documented the importance of the matrix on bird distributions (Hanson and Urban 1992; Pearson 1993; McGarical and McCombs

1995). These results support the importance of the matrix on species richness of grassland avifauna.

Interspersion juxtaposition is a measure of patch adjacency. This study demonstrates that more aggregated grassland patches increase grassland bird species richness. In models of species co-occurrence, ecologically similar species coexist via a tradeoff between exploration for and exploitation of resources (Brown 1989; Tilman 1994). This tradeoff implies that organisms must distribute themselves in order to maximize resource use; whereas maximizing resource use may require movement, or remain sedentary but be highly efficient foragers (Gordon 2000). Increase patch proximity, combined with the third most explanatory variable, a measure of total grassland area, indicates that the arrangement and amount of grassland habitat are important predictors of grassland bird species richness. Large, clustered patches of habitat increases the resources available while minimzing the risk of movement for exploiting those resources.

While no relationship between grassland bird species richness and grasshopper density and diversity was detected in this study, this does not mean that a relationship does not exist. It is well known that grasshoppers provide an important food resource to grassland birds. It is possible that the relatedness of grasshoppers to birds occurs at a finer scale then detectable in this study. It is also possible that the spatial correlation of grasshoppers occurs at a finer scale

then 30 meters. That being true, interpolation might not capture the fine scale variability, resulting in estimates that may not be characterizing the true density or diversity of grasshoppers along bird survey sites. While spatial interpolation provides estimates of data points that lack empirical data, this also introduces error variances (Issaaks and Srivastava 1989).

Wiens (1974, 1977) suggested that grassland birds are not limited by food; this speculation was supported by Gordon (2000), as well as this study. Perhaps there is a super-abundance of food in grasslands. While one food source may run low, species shift food sources to exploit the resources available. Grassland systems that are rainfall limited, such as that found in eastern Wyoming, are highly fluctuating, dynamic systems; resources therefore are variable and patchy making behavioral plasticity and flexibility a highly beneficial evolutionary strategy.

MANAGEMENT IMPLICATION

This study was an exploratory study at a broad scale. The results are designed to prompt further research into grassland bird community dynamics. Because of the nature of this study, no causal factors can be concluded; however, there is important strength in observational analysis. This study suggests that diverse edges increase species richness. This finding needs to be interpreted with caution. Although species richness of grassland may be higher in areas with greater high contrast edges, this study did not measure individual survival, fecundity or nest success. High contrast edges may be ecological traps or

population sinks as predator density can be considerably higher in edges (Oehler and Litvaitis 1996; Pedlar *et al.* 1997) and predators may use edges as travel corridors (Small and Hunter 1988). Therefore, high contrast edges may be detrimental to the viability of grassland birds, even though observed species richness can be high. If managers are concerned about overall grassland bird richness, regardless of species, than these results suggest that increasing the amount of high-contrast edges in the landscape would achieve this, although with a strong risk of creating population sink habitat. Because species richness measures do not explicity address which species are where, I speculate that more generalist species occur in areas with more high contrast edges, while specialists and interior species are supported by increased habitat amount and close aggregation of habitat patches. This speculation is based on the results of Penhollow and Stauffer (2000). Grassland bird species richness can be positively influenced by increases in pure habitat and increased patch proximity (less fragmentation). The positive influence of habitat and patch proximity found in this study on grassland birds concurs with other research (Gordon 2000).

Studies conducted at regional scales are important for uncovering broad patterns that may exist at only larger geographic scales (Wiens *et al.* 1987; Brown 1995). If patterns exist at these scales, the findings may be extremely useful to land managers that often have to make management decisions based on little

empirical data. The practicality of this study should not be overlooked. But the search for explanation into the cause of population declines of grassland birds will certainly require further research.

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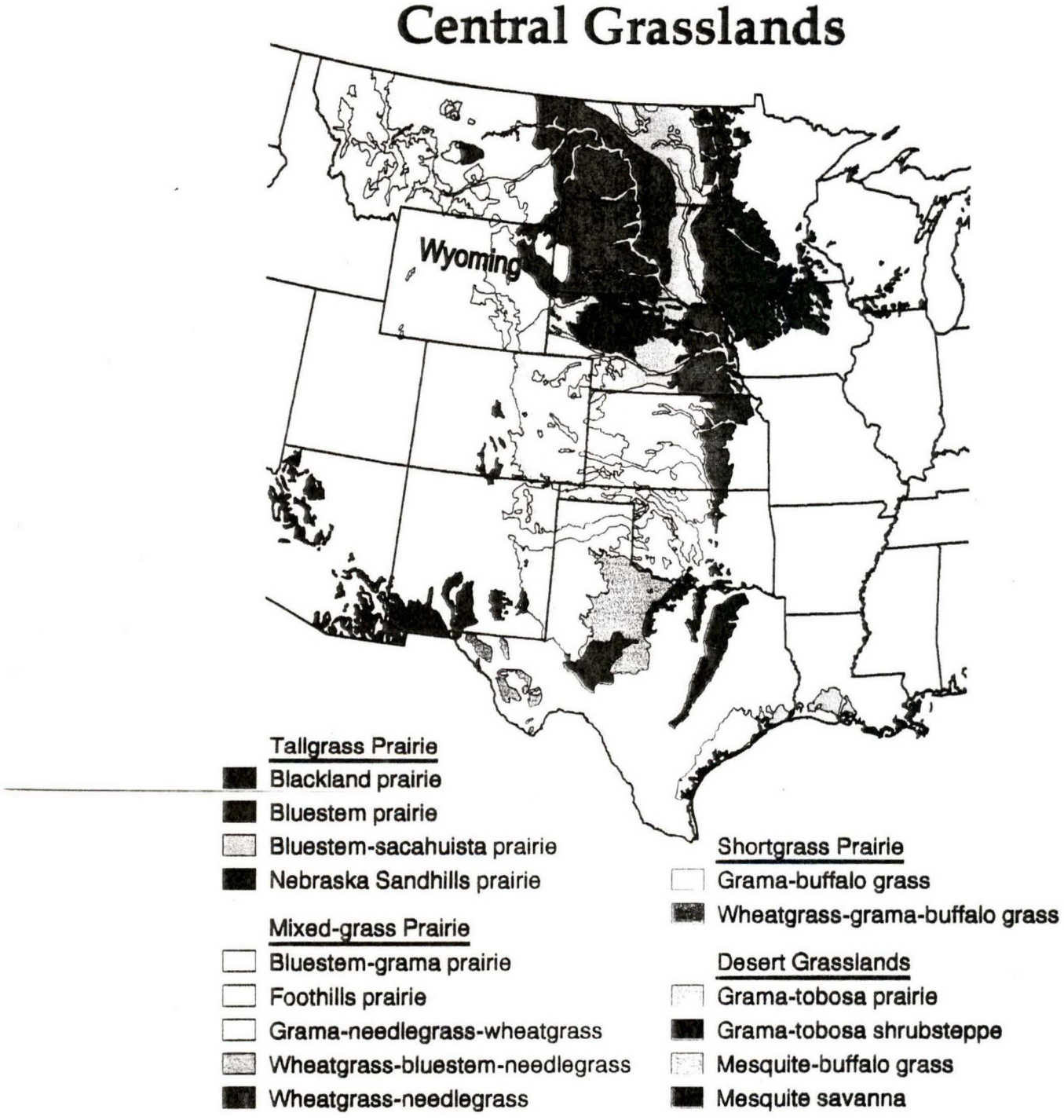

Figure 1: Central Grasslands of the United States.

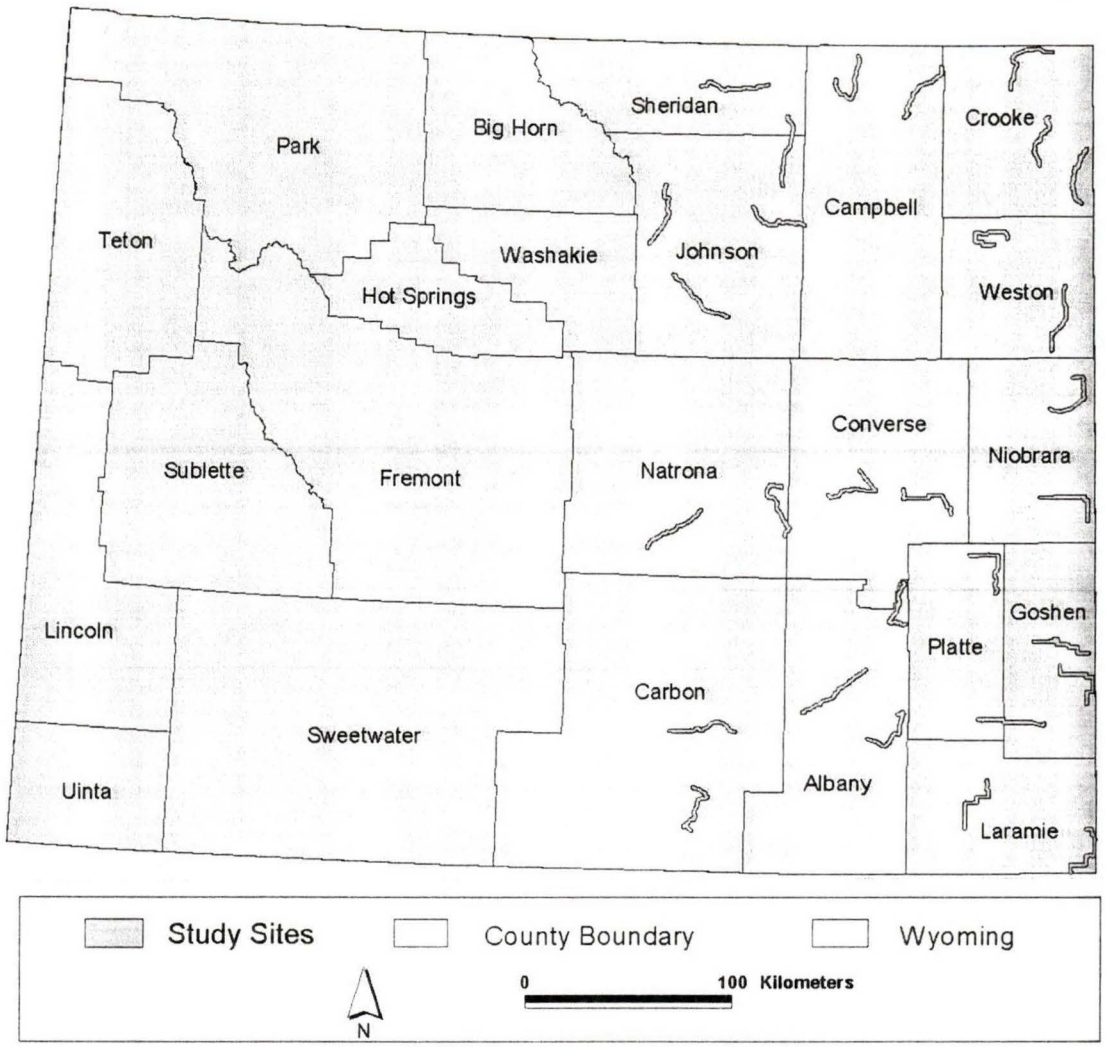

Figure 2: Study Area of Wyoming. Study Sites (N=29) shown on map.

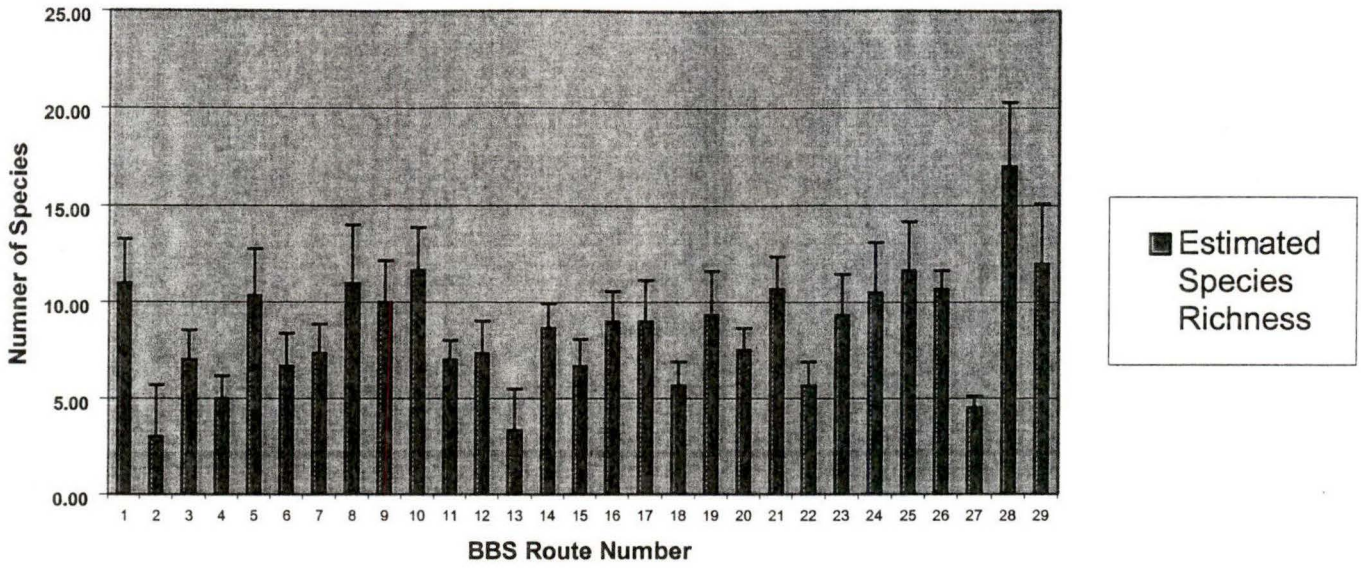

Figure 3: Estimated Species Richness by Site

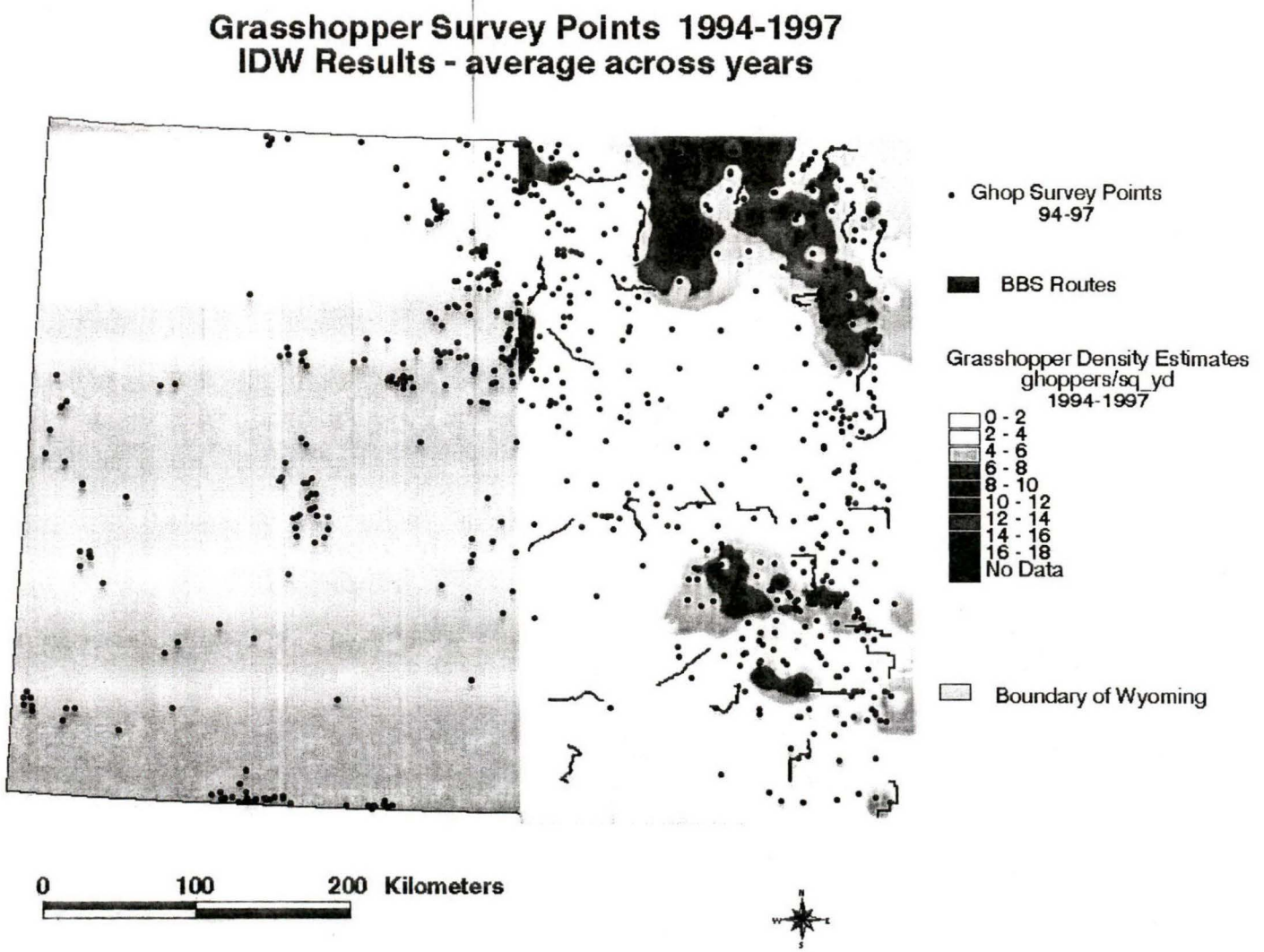

FIGURE 4: GRASSHOPPER DENSITY ESTIMATES ACROSS EASTERN WYOMING

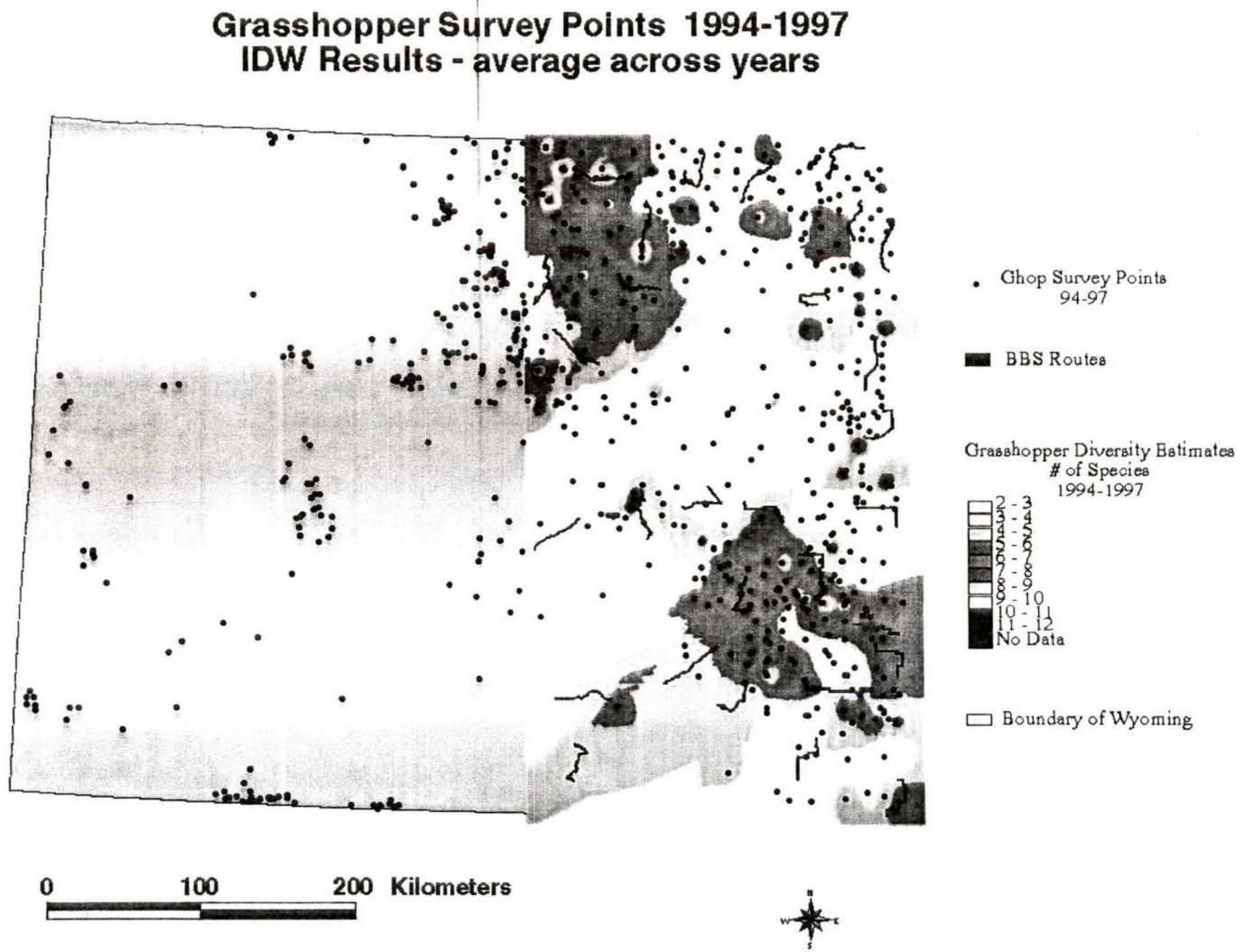

FIGURE 5: GRASSHOPPER DIVERSITY ESTIMATES ACROSS EASTERN WYOMING

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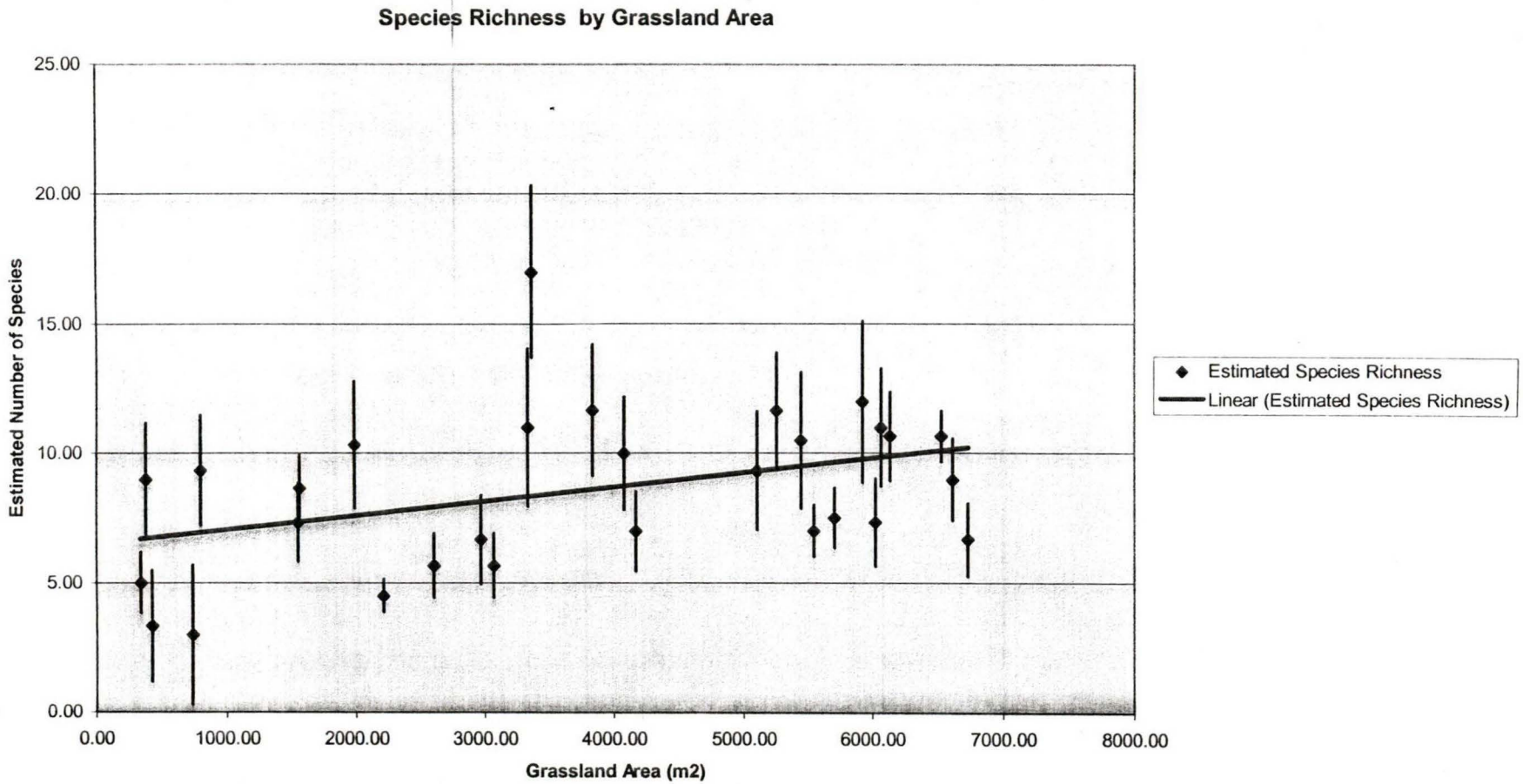

Figure 6: Species-Area Graph

TABLE 1: Grassland Bird Source Pool

Family Charadriidae Mountain Plover *Charadrius montanus* **Family Scolopacidae** Long-billed Curlew *Numenius americanus* Upland Sandpiper *Bartramia longicauda* **Family Accipitridae** Northern Harrier *Circus cyaneus* Ferruginous Hawk *Buteo regalis* Swainson's Hawk *Buteo swainsoni* **Family Falconidae** Prairie Falcon *Falco mexicanus* **Family Phasianidae** Ring-necked Pheasant *Phasianus colchicus* Sharp-tailed Grouse *Tympanuchus phasianellus* **Family Strigidae** Short-eared Owl *Asio Flammeus* Burrowing Owl *Athene cunicularia* **Family Caprimulgidae** Common Poorwil *Phalaenoptilus nuttallii*	**Family Alaudidae** Horned Lark *Eremophila alpestris* **Family Emberizidae** Grasshopper Sparrow *Ammodtamus savannarum* Baird's Sparrow *Ammodramus bairdii* Vesper Sparrow *Pooecetes gramineus* Savannah Sparrow *Passerculus sandwichensis* Lark Sparrow *Chondestes grammacus* Cassin's Sparrow *Aimophila cassinii* Field Sparrow *Spizella pusilla* Clay-colored Sparrow *Spizella pallida* Chestnut-collared Longspur *Calcarius ornatus* McCown's Longspur *Calcarius mccownii* Lark Bunting *Calamospiza melanocorys* Dickcissel *Spiza americana* **Family Icteridae** Bobolink *Dolichonyx oryzivorus* Western Meadowlark *Sturnella neglecta* Brewer's Blackbird *Euphagus cyanocephalus*

Table 2, Grassland Bird Species and Diet

Species	Diet
Upland Sandpiper	insects, seeds
Long-billed Curlew	insects, inverts
Mountain Plover	insects
Sharp-tailed Grouse	seeds, berries, insects
Ring-necked Pheasant	insects, inverts, small verts, seeds, grains, nuts
Northern Harrier	small verts, birds, snakes, frogs, insects (esp grasshoppers), carrion
Swainson's Hawk	small verts, rabbits, lizards, snakes, frogs, toads, birds, occ feed heavily on large insects
Ferruginous Hawk	small mammals, snakes, lizards, large insects
Prairie Falcon	birds, small mammals, insects, lizards
Short-eared Owl	rodents, birds, insects
Burrowing Owl	insects, rodents, lizards, birds
Common Poorwill	insects
Horned Lark	seeds, insects -spiders, snails, grass and forb seeds
Bobolink	insects, seeds - few spiders, grass and forb seeds. Young fed insects almost exclusively.
Western Meadowlark	insects, spiders, sowbugs, snails, grass and forb seeds.
Brewer's Blackbird	insects, spiders - also crustaceans, snails, grass and some forb seeds.
Chestnut-collared Longspur	insects, seeds - spiders, grass, forb and sedge seeds. Young fed 100% insects.
McCown's Longspur	seeds, insects- grass and ford seeds. Young fed all or mostly insects.
Vesper Sparrow	insects, seeds: 50% insects, 50% seeds
Savannah Sparrow	insects, seeds, snails - spiders; seeds mostly grass
Baird's Sparrow	insects, seeds -spiders, grass and for seeds. Young fed 100% insects.
Grasshopper Sparrow	insects, seeds, inverts -grass and forb seeds.
Lark Sparrow	seeds, insects -grass and forb seeds
Clay-colored Sparrow	insects, seeds - forb and grass seeds; also catkins, deciduous tree buds in winter
Field Sparrow	insects, seeds - few spiders, seeds of forbs and grass. Young fed 100% insects, spiders.
Cassin's Sparrow	insects, seeds -insects during breeding season; grass and forb seeds seeds
Diskcissel	insects, seeds -young birds predominately (70%) grain, grass, and forb seeds, rest insects.
Lark Bunting	insects, seeds - grasshoppers, grass and forb seeds.

Table 3: Modified Anderson II Classification

Level I	Level II
(1) Urban	1.1 Residential
	1.2 Commercial, Industrial, Transportation (Roads)
(2) Agricultural	2.1 Pasture, Alfalfa, Hay – irrigated
	2.2 Row Crops
	2.3 Small grains
	2.4 Fallow
(3) Natural/Semi	3.1 Herbaceous Natural/Semi-natural Grassland
	3.2 Shrub and Brushland
(4) Forestland	4.1 Deciduous Forest
	4.2 Evergreen Forest
(5) Open Water	5.1 Water
(6) Wetland	6.1 Herbaceous Wetland
	6.2 Wooded Wetland
(7) Barren Land	7.1 Bare Ground, Rocks, Clay
	7.2 Strip Mines, Gravel Pits

Table 4: Grassland Habitat Metrics

Variables	Definition	Metric
GA	Total Grassland Area	Amount
NP	Total Number of Patches	Patch Level
AREA (mean)	Mean Patch Area in 'grassland'	
TE	Total Edge	Edge/Boundary
CWED	Contrast with Matrix	
PARATIO	Perimeter/Area Ratio	
FRACTAL	Mean Fractal Dimension	
ENN	Euclidean Nearest Neighbor	Proximity
PROXIMITY	Mean Proximity w/n 500 meters	
SIMILARITY	Similarity Index w/n 500 meters	
IJI	Interspersion/Juxtaposition	

Table 5: **Simulations = 10000**

Results of the empirical distribution analysis

Inter-event Distances: **Percent rank of the deviation between observed richness and the mean of 10000 simulations**

YEARS 1994-1998

BBSRoute	Obs.Richness	mean Sim	stdev (sim)	dev	sqdev	rank	%rank
5	12	11.5537	1.329546193	-0.4463	0.19918369	7110	0.71092891
7	4	5.2285	0.740366507	1.2285	1.50921225	101	0.01009899
19	7	13.5102	1.366119537	6.5102	42.38270404	1	0.00009999
26	7	13.4647	1.259965341	6.4647	41.79234609	1	0.00009999
28	13	13.5632	1.309876841	0.5632	0.31719424	4417	0.44165583
42	6	13.5221	1.33367517	7.5221	56.58198841	1	0.00009999
43	9	13.4608	1.356999449	4.4608	19.89873664	2	0.00019998
44	12	13.5305	1.306690665	1.5305	2.34243025	1185	0.11848815
45	12	13.591	1.336524459	1.591	2.531281	1279	0.12788721
46	11	13.5696	1.279812342	2.5696	6.60284416	123	0.01229877
48	8	13.593	1.434836881	5.593	31.281649	1	0.00009999
49	9	13.5388	1.257637756	4.5388	20.60070544	1	0.00009999
50	5	3.6758	0.513537469	-1.3242	1.75350564	224	0.02239776
63	10	13.5069	1.378674169	3.5069	12.29834761	61	0.00609939
68	8	13.5013	1.289870027	5.5013	30.26430169	1	0.00009999
69	12	13.5366	1.391421592	1.5366	2.36113956	1520	0.15198480
83	10	13.441	1.328343122	3.441	11.840481	83	0.00829917
87	7	13.4854	1.369589142	6.4854	42.06041316	1	0.00009999
88	10	13.4603	1.337984652	3.4603	11.97367609	101	0.01009899
89	9	13.5415	1.29917148	4.5415	20.62522225	1	0.00009999
90	14	13.468	1.336470956	-0.532	0.283024	4497	0.44965503
91	7	13.3519	1.31340736	6.3519	40.34663361	1	0.00009999
104	8	13.5925	1.403438889	5.5925	31.27605625	1	0.00009999
107	9	13.5253	1.329713023	4.5253	20.47834009	1	0.00009999
108	13	13.5008	1.304518891	0.5008	0.25080064	4503	0.45025497
110	13	13.5365	1.367645713	0.5365	0.28783225	4892	0.48915108
111	5	13.537	1.297073336	8.537	72.880369	1	0.00009999
112	17	13.4263	1.384182035	-3.5737	12.77133169	21	0.00209979
120	12	11.7094	1.338032389	-0.2906	0.08444836	7079	0.70782922

Table 6: Accuracy Assessment

	Reference Data														
Classified Data	Residential	Commercial	Crop	Row Crop	Small Grain	Fallow	Grassland	Shrub	Deciduous	Evergreen	Water	Woody Wetland	Herb Wetland	Bare rock	Row Totals
Low Intensity Residential	14														14
Commercial, Industrial, Transportation		32					1	3							36
Cropland, Pasture, Hay			41			1			1			3			46
Row Crops				11											11
Small Grains			2		9	1									12
Fallow		1			2	28	2							2	35
Herb (Grass)Natural/Seminatural		1	2				64	23							90
Shrub and Brush Land		2	1			1	16	71	1			2		2	96
Deciduous Forest			1					1	21	4	1	6			34
Evergreen Forest								1	3	23		1			28
Water											24				24
Woody Wetland			2					1				17	3	1	24
Herbaceous Wetland							1					1	15		17
Bare rock, sand, clay		1	1			1		6					1	21	31
Strip Mines															0
Transitional								2	1						3
Column Totals	14	37	50	11	11	32	84	108	27	27	25	30	19	26	501

Table 11: Regressor Variable Weights

Weights by Variable

Variable:	Weights*
CWED	0.7245
IJI	0.5193
CA	0.3920
FRAC_MN	0.3862
ENN_MN	0.3712
Proxim_MN500m	0.3543
AREA_MN	0.2804
PARATIO_MN	0.2604
TE	0.2600
NP	0.2000
Sim_Mn500m	0.1982

* evidence for importance of regressor variable
* = sum of Akaike weights for all models containing given regressor variable